# FLOWERS AND INSECTS. XIX.

CHARLES ROBERTSON.

I. *Comparison of the genera of bees observed in Low Germany and in Illinois, with the number of species of each and their flower visits.*—The results credited to Müller are taken from the *Fertilization of Flowers.* They are based on observations made by Herr Borgstette at Teklenburg, in the north of Westphalia, and by Müller at Lippstadt and in Sauerland, in the central and southern parts of the same region, as well as observations made by him in Thüringia. My results are based on observations made within ten miles of Carlinville. Each species of bee is credited with a visit for each of the species of plants on whose flowers it has been taken.

II. *On the flower visits of oligotropic bees.*—Those bees which visit a wide circle of flowers Loew[1] calls polytropic. On the other hand, the bees which restrict their visits to a few flowers he calls oligotropic. Cases are given by quite a number of authors, but, as far as I can learn, they are cited as mere curiosities; and, as if to keep them more interesting by surrounding them with mystery, the facts which give them significance are omitted. The fact that a species of bee is found on the flowers of one or a few species of plants may only indicate that the bee is rare, or that the entomologist does not know where to look for it. In the economy of the host-bees (those not inquiline) the most important flowers are those from which the female gets the pollen upon which her brood is fed, and we need not trouble ourselves with any cases, or give special names to them, unless it is particularly specified that the female collects the pollen. The more often the female visits a flower without collecting any pollen, the stronger becomes the presumption that there is

[1] Blumenbesuch von Insekten an Freilandpflanzen. Jahr. Bot. Gartens Berlin 3:—. 1884.

| | Westphalia and Thüringia | | Macoupin County, Illinois | |
|---|---|---|---|---|
| | No. species | Visits | No. species | Visits |
| Sphecodes | 17 | 28 | 12 | 74 |
| Prosopis | 15 | 88 | 7 | 118 |
| Colletes | 4 | 16 | 14 | 96 |
| Halictus | 32 | 440 | 30 | 961 |
| Augochlora | — | — | 5 | 232 |
| Agapostemon | — | — | 4 | 132 |
| Andrena | 51 | 219 | 42 | 419 |
| Parandrena | — | — | 1 | 13 |
| Nomia | — | — | 1 | 7 |
| Panurginus | — | — | 9 | 52 |
| Perdita | — | — | 1 | 3 |
| Calliopsis | — | — | 3 | 39 |
| Rhophites | 2 | 8 | — | — |
| Rhophitoides | 1 | 2 | — | — |
| Halictoides | 1 | 2 | 1 | 4 |
| Panurgus | 2 | 16 | — | — |
| Dasypoda | 1 | 7 | — | — |
| Cilissa | 3 | 16 | — | — |
| Macropis | 1 | 4 | 1 | 6 |
| Ceratina | 1 | 3 | 2 | 154 |
| Xylocopa | — | — | 1 | 2 |
| Eucera | 1 | 15 | — | — |
| Emphor | — | — | 1 | 4 |
| Melissodes | — | — | 18 | 266 |
| Synhalonia | — | — | 4 | 83 |
| Xenoglossa | — | — | 2 | 5 |
| Entechnia | — | — | 1 | 5 |
| Anthophora | 5 | 32 | 5 | 52 |
| Saropoda | 1 | 9 | — | — |
| Melecta | 2 | 3 | 1 | 1 |
| Bombomelecta | — | — | 1 | 1 |
| Crocisa | 1 | 1 | — | — |
| Epeolus | 1 | 2 | 12 | 113 |
| Nomada | 21 | 85 | 17 | 130 |
| Heriades | 1 | 13 | 3 | 34 |
| Chelostoma | 3 | 25 | — | — |
| Andronicus | — | 1 | 1 | 8 |
| Alcidamea | — | — | 2 | 32 |
| Osmia | 13 | 100 | 10 | 102 |
| Megachile | 9 | 77 | 15 | 225 |
| Chalcodoma | 1 | 1 | — | — |
| Diphysis | 1 | 15 | — | — |
| Anthidium | 3 | 16 | 1 | 3 |
| Stelis | 3 | 12 | 2 | 7 |
| Coelioxys | 6 | 28 | 7 | 66 |
| Neopasites | — | — | 2 | 4 |
| Bombus | 13 | 457 | 8 | 456 |
| Psithyrus | 4 | 52 | 3 | 12 |
| Apis | 1 | 189 | 1 | 157 |
| Totals | 205 | 1,981 | 251 | 4,078 |
| Not accounted for | | 210 | | |
| | | 2,191 | | |

another flower which she does visit for that purpose, and which, therefore, holds a more important relation to her species. Accordingly, I propose to consider those examples in which the female collects pollen of one species, or several species of the same genus or natural family, the relationship of the plants being such as to give significance to the cases. On the other hand, if a bee uses the pollen of only two plants of different families, I assume that it is essentially polytropic, and that the few visits are merely connected with the fact that it is rare or has a short flight. Of course there still remains a strong contrast between the visits of a bee which flies only a month or two and one which flies throughout the season. As a rule, if a bee has a long flight it must be regarded as polytropic, unless the flowers on which it depends have a long blooming time. Of the thirty-nine species of Halictus and the allied Augochlora and Agapostemon, I regard only one as oligotropic, *Halictus nelumbonis*. It has a comparatively short flight, while the blooming seasons of the Nymphæaceæ are long. When a genus of plants has more than one closely allied species, the difference between a monotropic and an oligotropic bee may depend merely upon the accident that only one species occurs in the neighborhood. My observations show that an oligotropic American bee will gather the pollen of a closely related introduced European plant of the same genus.

The relations of the host-bees to the flowers from which they get pollen are quite analogous to the relations of parasites to their hosts, of phytophagous insects to their food plants, or of predaceous insects to the insects upon which they feed or with which they provision their nests. How the bees maintain these relations is much easier to understand, since the flowers are modified in such a way as to facilitate their visits.

Any ecological position is of advantage only to a limited number of individuals. As soon as this *optimum* number is passed, anything which will enable a set of individuals to get along without coming into competition with the dominant form will be of advantage to them, and their preservation will depend upon their adopting this course. A characteristic which would be a disadvantage before the *optimum* is reached, may be an advantage after the *optimum* is passed. Whatever may be the characteristic which enables this set of individuals to hold its own in a new ecological position, I think the principal circumstance which accounts for the adoption of a new mode of life is the pressure of competition. The dominant form retains the original position, the other becomes modified (specialized) in adaptation to the newly acquired position.

In my neighborhood there are thirty-five species of Andrena, which complete their flight from March 17 to July 14. These succeed one another, so that not more than twenty-one would be in competition at the same time, if their habits were the same. Ten begin their flight in March, seventeen in April, seven in May, and one in June.

Of thirty-three species whose habits are pretty well known, nineteen are polytropic and fourteen oligotropic, in the sense in which I use those terms. Four of the oligotropic species get pollen from plants of the same genus, but each of the other ten has its own flower, so there are eleven sets which are absolutely without competition among themselves. I think it is clear that so many species could hardly flourish in the same locality and complete their flight in so short a time, if all were in competition for the pollen of the same flowers.

The average maximum flight of the females is forty-eight days. Now suppose that, on account of the pressure of competition, one of these shifts to a different phenological position. Of the flowers whose pollen is so situated that the bee can readily collect it, only those are available whose pollen is produced in abundance between the time the female is impregnated and the end of the time of flight. To use human terms, the bee must choose between a limited number of flowers, and is in no wise free to regulate its habits according to mere whim.

From the above considerations I do not accept the views of Kerner,[2] although they are the ones adopted by Knuth[3] to

[2] Natural History of Plants **2**: 206. 1894.

[3] Handbuch der Blütenbiologie **1**: 106, 114. 1898.

explain such cases. Kerner says: "The flowers of the common bryony, *Bryonia dioica*, are not less remarkable. They occur on two kinds of plants, *i. e.*, on one plant are developed only staminate and on the other only pistillate flowers, and since the pollen is not powdery, and therefore not scattered by wind, it must be carried by insects from plant to plant if the ovules are to mature. But the flowers, especially the pistillate ones, are very insignificant, green in color, with faint smell, and they are half hidden under the foliage. Many insects fly past them without noticing them. They are almost exclusively visited by one of the Hymenoptera, viz., *Andrena florea*, and it can find them in the most out-of-the-way places. This can hardly be accounted for except by supposing that the scent of bryony flowers is perceived by these particular bees and not by other insects." He admits these conclusions must be accepted with discretion. *Andrena florea* gets its pollen exclusively from staminate plants of bryony. How much better do we understand the case if we admit that the scent of the flowers is perceived by the bee? Tne mud-dauber makes its nests of mud and fills them with flower-spiders, which are so near like the color of the flowers which they frequent that they are enabled to capture their prey by lying in wait. Do we explain the case if we say that Pelopœus perceives the scent of mud and Thomisidæ?

As for out-of-the-way places, my observations indicate that, as a rule, oligotropic bees nest in the neighborhood where their food plants occur, and that, when the brood emerges next year, it finds the flowers in bloom, and that near by.

As a typical case of an oligotropic bee, *Emphor bombiformis* may be mentioned. Both sexes occur in abundance on flowers of *Hibiscus lasiocarpus*, the female collecting the pollen, the males often spending the night in the flowers. The bees do not occur except when the Hibiscus is in bloom. Within several yards of the Hibiscus I have seen the female making nests in a dry bank, carrying water to soften the earth she was excavating. The bees coming out next year find the Hibiscus in bloom near by. The only visits to other flowers I have seen the bees make were to those in the neighborhood of the Hibiscus. Thus I have seen a single female sucking the nectar of *Cephalanthus occidentalis*, and another that of *Vernonia fasciculata*, as well as a single male sucking nectar of *Ipomœa pandurata*. The outside visits in no way modify the essential relation of the bee to the Hibiscus. For myself, I do not believe in the absolutely exclusive visits of oligotropic bees to their pollen flowers, and I see no reason why they should be expected. If the plants from which a bee gets pollen are common and widely distributed, the proportion of flowers to which it occasionally resorts is much greater than in a case like Hibiscus. Indeed, it strikes me that it is an advantage for the males and unimpregnated females to visit other flowers and not interfere with the females which are collecting pollen. Some bees which stick their pollen with honey get the pollen from nectarless flowers, and so are compelled to visit other flowers for nectar. I have seen *Macropis steironematis*, with pollen balls on her legs, sucking nectar of *Melilotus alba*.

In case of this Macropis and Steironema, Kerner might say the bee perceived or liked yellow flowers, but all of the accessory visits I have seen this bee make were to white flowers, Ceanothus, *Melilotus alba*, Apocynum. In these cases Steironema was in bloom in the neighborhood.

I shall now give the cases of oligotropic bees mentioned by Lubbock,[4] on authority of Müller; by Loew,[5] on authority of Schmiedeknecht; and by Knuth[6] from various sources.

| | | | |
|---|---|---|---|
| Andrena florea | visits exclusively | | Bryonia dioica. |
| hattorfiana | " | " | Scabiosa (Knautia) arvensis. |
| Halictoides | " | " | Campanula spp. |
| Cilissa melanura | " | " | Lythrum Salicaria. |
| Macropis labiata | " | " | Lysimachia vulgaris. |
| Osmia adunca | " | " | Echium. |

[4] British Wild Flowers in Relation to Insects 21. 1875.

[5] Blumenbesuch von Insekten an Freilandpflanzen. Jahrb. Bot. Gartens Berlin 3:274 (72). 1884.

[6] Handbuch der Blütenbiologie 1:114. 1898.

| | | |
|---|---|---|
| Andrena nasuta | visits | Anchusa officinalis. |
| cineraria | " | Salix. |
| lapponica | " | Vaccinium. |
| cettii | " | Scabiosa (Knautia). |
| hattorfiana | " | Scabiosa. |
| florea | " | Bryonia. |
| alpina | " | Campanula. |
| curvungula | " | Campanula. |
| austriaca | " | Umbelliferæ. |
| lucens | " | Umbelliferæ. |

| | | |
|---|---|---|
| Andrena florea | visits exclusively | Bryonia dioica. |
| hattorfiana | " " | Scabiosa (Knautia) arvensis. |
| cettii | " " | Scabiosa (Knautia) arvensis. |
| nasuta | " " | Anchusa officinalis. |
| Bombus gerstaeckeri | " " | Aconitum lycoctonum. |
| Cilissa melanura | almost " | Lythrum Salicaria. |
| Macropis labiata | " " | Lysimachia vulgaris. |
| Osmia adunca | " " | Echium. |
| cementaria | " " | Echium. |

*Andrena florea*, mentioned in the three lists, collects pollen of bryony and has been found on no other flowers.

*Andrena hattorfiana:* both sexes visit *Scabiosa arvensis*, the female collecting pollen. Müller found a female on *Dianthus carthusianorum* and a male on *Jasione montana*.

*Halictoides dentiventris:* Müller captured both sexes on *Campanula rotundifolia* and *trachelium*, but not collecting pollen. He says that at St. Petersburg Morawitz found it only on Campanula. In the Alps, Müller observed this species collecting pollen of *Potentilla grandiflora* and *Hypochœris uniflora* and visiting seven other flowers.

*Cilissa melanura* collects pollen of *Lythrum Salicaria*, the males sucking. Müller saw the female sucking on flowers of *Leontodon hirtus*.

*Macropis labiata:* males and females visit *Lysimachia vulgaris*, the females collecting pollen. Males suck on *Œnanthe fistulosa*, *Rhamnus frangula*, *Rubus fruticosus*.

*Osmia adunca:* Müller saw both sexes on *Echium vulgare* and says it feeds its young exclusively on honey and pollen of

Echium, but under *Vicia Cracca* this species is indicated as collecting pollen. In the Berlin garden Loew found it collecting pollen of *Nepeta Mussini.* In the two latter cases there is some error, or the bee is not oligotropic. So of the cases mentioned by Lubbock, only one is exclusive, and two are not even oligotropic.

*Andrena cettii:* females collect pollen of *Scabiosa arvensis.*

*Bombus gerstaeckeri:* why Knuth says this species visits exclusively *Aconitum lycoctonum* I do not know, for on page 191 it is distinctly stated that the males and workers visit *A. Napellus,* but nothing is said about pollen-collecting.

*Osmia cementaria:* males and females suck and collect pollen on *Echium vulgare;* males suck on *Trifolium arvense.*

Of the cases mentioned by Knuth, excepting *Andrena nasuta,* only two are exclusive. *Osmia adunca* and *Bombus gerstaeckeri* are not good cases. In the other cases the females collect the pollen exclusively from the plants set opposite them, and the cases are not essentially modified by occasional visits for nectar to other flowers. I hold that *Macropis labiata* is as good a case as *Andrena florea.*

Of the cases mentioned by Loew, three have been passed upon. I know of nothing against any of them except *Andrena cineraria.* The female collects pollen of Salix, but also of *Taraxacum officinale,* so I should exclude it.

In the observation of the insect visits of flowers correct determinations are very important, for otherwise the records are wrong. One has to be sure that the bee is actually collecting pollen, for often a female bee will suck nectar from a flower when her scopæ are full of pollen from another species. On the other hand, there is danger of assuming that a bee is oligotropic from too few observations.

A neighborhood where the flora and insect fauna are in their normal condition is more favorable for correct observations on oligotropic bees; for, when the flowers upon which a bee depends become extinct or rare, the bee may disappear or be forced to resort to flowers which originally it did not visit. In most cases the former is more likely to happen.

A bee may be regarded as oligotropic: (1) When the female collects the pollen of the plants in question and is not known to collect pollen of any other plants. (2) When the bee does not occur except during the blooming season of the flowers. If the female is shown to occur after the flowers have quit blooming, the case is very doubtful. (3) When the bee is frequent upon the flowers, and more or less rare upon other flowers, at any rate except in the neighborhood of the food flowers. The case is also doubtful if it is shown that the distribution of the bee extends greatly beyond the plants upon which it is supposed to depend.

In the more satisfactory cases, if any one should say that he had observed the bee collecting pollen from a quite unrelated flower, I would not accept the determination, or, if that were beyond question, the opinion that the pollen came from the flower on which the bee was taken.

Below I give a list of bees which I regard as oligotropic in the above sense. When I have observed the female collecting pollen from more than one species of a genus, I give the genus; when from more than one genus, I give the family. The details will be given elsewhere.

In Prosopis the females are destitute of pollinigerous apparatus, their nests being provisioned with a paste of honey and pollen. I know of no way to distinguish the flowers which the females visit for this purpose from those which they visit in only an incidental way, so I assume that a species of this genus is oligotropic only so long as it is found exclusively on flowers of one species or group. This may be assumed for either sex so long as the condition holds, as in case of *P. illinoensis*, of which I do not know the females. *P. nelumbonis* has always seemed to me to be the best case of an oligotropic Prosopis.

I have never believed that our species of Epeolus were cuckoos of Colletes, because there are more common species of the former than of the latter genus, and their phenological positions do not show the same correlations which exist between Andrena and Nomada, Megachile and Coelioxys. Besides, the maximum of Epeolus does not approximate that of any other

| Bee | Plants visited by females for pollen | Number of species | Flowers of same genus visited for nectar | Flowers of same family visited for nectar | Other flowers visited for nectar | Total flowers visited for nectar |
|---|---|---|---|---|---|---|
| Colletes aestivalis | Heuchera hispida | 1 | — | — | 4 | 4 |
| latitarsis | Physalis | 3 | — | — | 6 | 6 |
| willistonii | Physalis lanceolata | 1 | — | — | 3 | 3 |
| americanus | Compositæ | 8 | — | 2 | 3 | 5 |
| armatus | " | 4 | — | 1 | 1 | 2 |
| compactus | " | 8 | — | 2 | — | 2 |
| eulophi | " | 3 | — | 3 | 11 | 14 |
| Andrena arabis | Arabis lævigata | 1 | — | — | — | — |
| erigeniæ | Claytonia Virginica | 1 | — | — | 2 | 2 |
| geranii | Hydrophyllum appendic'um | 1 | — | — | 2 | 2 |
| g. maculati | Geranium maculatum | 1 | — | — | 1 | 1 |
| polemonii | Polemonium reprans | 1 | — | — | 2 | 2 |
| spiræana | Spiræa Aruncus | 1 | — | — | 3 | 3 |
| violæ | Viola cucullata | 1 | 2 | — | 3 | 5 |
| erythrogastra | Salix | 4 | 1 | — | 7 | 8 |
| illinoensis | " | 4 | 1 | — | 8 | 9 |
| mariæ | " | 4 | — | — | 6 | 6 |
| salicis | " | 4 | — | — | 2 | 2 |
| nasonii | Umbelliferæ | 3 | — | — | 1 | 1 |
| ziziae | " | 5 | — | — | — | — |
| rudbeckiæ | Rudbeckia hirta | 1 | — | 1 | — | 1 |
| aliciæ | Compositæ | 5 | — | 2 | — | 2 |
| asteris | " | 3 | — | — | 1 | 1 |
| helianthi | " | 3 | — | 2 | — | 2 |
| nubecula | " | 4 | — | 1 | — | 1 |
| pulchella | " | 6 | — | 2 | — | 2 |
| solidaginis | " | 6 | — | 1 | 1 | 2 |
| Parandrena andrenoides | Salix | 3 | 1 | — | 9 | 10 |
| Macropis steironematis | Steironema | 3 | — | — | 3 | 3 |
| Halictus nelumbonis | Nymphæaceæ | 3 | — | — | — | — |
| Megachile exilis | Campanula Americana | 1 | — | — | 6 | 6 |
| pugnata | Compositæ | 4 | — | 1 | 3 | 4 |
| Panurginus labrosus | Rudbeckia triloba | 1 | — | 2 | — | 2 |
| albitarsis | Compositæ | 2 | — | 4 | — | 4 |
| asteris | " | 4 | — | — | — | — |
| compositarum | " | 5 | — | 3 | 1 | 4 |
| labrosiformis | " | 7 | — | 3 | — | 3 |
| rudbeckiæ | " | 4 | — | — | — | — |
| rugosus | " | 4 | — | 2 | — | 2 |
| solidaginis | " | 2 | — | 4 | — | 4 |
| Xenoglossa pruinosa | Cucurbita Pepo (cult.) | 1 | — | 3 | — | 3 |
| Emphor bombiformis | Hibiscus lasiocarpus | 1 | — | — | 3 | 3 |
| Anthophora walshii | Cassia Chamæcrista | 1 | — | 1 | 4 | 5 |
| Perdita octomaculata | Compositæ | 3 | — | — | — | — |
| Halictoides marginatus | Helianthus | 3 | — | 1 | — | 1 |

| Bee | Plants visited by females for pollen | Number of species | Flowers of same genus visited for nectar | Flowers of same family visited for nectar | Other flowers visited for nectar | Total flowers visited for nectar |
|---|---|---|---|---|---|---|
| Mellisodes desponsa - | Cnicus - - - - | 2 | 1 | — | 1 | 2 |
| illinoensis - | Lepachys pinnata - | 1 | — | — | 1 | 1 |
| agilis - - | Compositæ - - - | 6 | — | 12 | 10 | 22 |
| americana - | " - - - | 9 | — | 2 | 1 | 3 |
| coloradensis - | " - - - | 7 | — | 6 | 1 | 7 |
| pennsylvanica | " - - - | 6 | — | 9 | 3 | 12 |
| simillima - | " - - - | 6 | — | 12 | 3 | 15 |

genus of bees on which it might be supposed to be inquiline. Then they are more abundant than would be expected of inquiline bees. Mr. Ashmead's observations confirmed my views, and I have never doubted their correctness since I first read an account of them. In *Psyche*, for March 1894, p. 41, he states that he found *E. donatus* making nests in the ground and provisioning them with a honey-paste. Epeolus thus comes under the same category as Prosopis and is treated the same way in the table.

The cuckoo bees of the genus Nomada hold no particular relations to flowers except through their hosts. However, they show considerable differences. *N. vincta*, which is common on Helianthus and was taken once on Coreopsis, is, I think, an inquiline of *Andrena helianthi*, both bees occurring at the same time, in the same neighborhood, and on the same flowers.

| Bee | At least females visit exclusively | No. spp. | Other fls. visited by male |
|---|---|---|---|
| Prosopis nelumbonis - | Nymphæaceæ - - - - | 2 | — |
| thaspii - - | Thaspium aureum trifoliatum - | 1 | — |
| illinoensis - - | Umbelliferæ - - - - | 5 | — |
| Epeolus helianthi - | Helianthus grosse-serratus - | 1 | 1 |
| compactus - | Compositæ - - - - | 4 | — |
| cressonii - | Compositæ - - - - | 13 | 3 |
| pectoralis - - | Compositæ - - - - | 2 | — |
| pusillus - | Compositæ - - - - | 4 | — |
| Nomada vincta - - | Compositæ - - - - | 3 | — |

III. *Competition of flowers for the visits of bees.*— It is a question to what extent groups of plants adapted to certain kinds of bees should be regarded as in competition and to what extent they should be regarded as mutually helpful. We will suppose a case in which a plant whose flowers may be visited by bees is introduced into a region where all visitors must be acquired. If the region contains no flowers, there will be no bees to acquire. On the other hand, it seems to me that the more nearly the flora retains its original characteristics the more bees there will be and the more chances there will be of the new flower acquiring bees as visitors. My view is that a patch of plants adapted to bees of certain kinds will be more abundantly visited, if it is surrounded by plants depending on bees of the same kinds, than if the neighboring grounds are unoccupied. There will be more of these bees in the neighborhood. In the table there are fifty-two species which get pollen from particular plants. As far as the data are correct, we take it for granted that the presence and abundance of these bees in a given locality depend on the presence and abundance of the flowers from which they get their pollen. One object in making the table is to show that the plants growing in the neighborhood of plants visited by oligotropic bees gain a certain number of bee visits. The table shows that these plants gain 204 visits in this way. It is expected, however, that some of the visits enumerated in the second and third columns will have to be transferred to the first. Excluding these columns, the neighboring unrelated plants gain 116 visits from the proximity of the food-plants of oligotropic bees. It is not likely that a plant suited to the visits of different kinds of bees will show the normal circle of visitors unless it holds its normal position in the original flora.

IV. *On the influence of bees in the modification of flowers.*— The facts indicate that the first entomophilous flowers were visited for nectar. Anemophilous flowers offer such a poor foothold for insects that they are very seldom visited by them, and the pollen, although no doubt palatable to many insects, is so light and dry that it is apt to be blown away as soon as it is liberated from the anthers. The first step in the development of entomophilous flowers was the secretion of nectar somewhere about the stamens and pistils, correlated with the modification of the flower so as to afford convenient resting places for insects, and the pollen becoming more adhesive, so that it would remain on the anthers after dehiscense and become attached finally to the bodies of the guests. The object of insect visits being the nectar, modifications favoring cross-pollination resulted in the various forms of diclinism and dichogamy. The perfection of nectar-bearing flowers naturally reached a high grade in the less specialized groups of plants, as, for example, the orchids, and was most frequently associated with the less specialized anthophilous insects.

Along with the development of convenient landing places and sticky pollen, there has no doubt been an increasing number of insects which resorted to flowers for pollen. Finally, the most highly specialized of anthophilous insects, the Hymenoptera, gave rise to a still more highly specialized group of insects which adopted the habit of provisioning their nests with nectar and pollen. Along with the acquisition of this habit the bees developed a coat of feathery hairs to which the pollen might cling, these hairs on certain parts of their bodies, as the hind legs and ventral surface of the abdomen, being greatly modified to form special pollen-carrying apparatus called scopæ. Thus the pollen became absolutely essential in the economy of the most highly specialized anthophilous insects. To the flowers, on the other hand, the bees became the most important visitors, because they had to resort to flowers more frequently than other insects, and because they were provided with a coat specially fitted to retain the pollen, and at the same time exerted themselves to get the coat as full of pollen as possible.

That the development of entomophilous flowers with sticky pollen preceded the development of the bees is indicated by the fact that the less specialized bees only collect adhesive pollen. The most highly specialized bees, however, have acquired the habit of sticking the pollen with honey, and so can use that of anemophilous plants.

Those flowers, however, which, through their nectar and correlated modifications, were the best fitted to use the services of ordinary insects for cross-pollination, were the least fitted to utilize the insects which were the highest product of anthophilous development. Strange as it may seem, the characters which hindered them from availing themselves of these services were the very characters which are considered the highest adaptations for cross-pollination, viz., diclinism, dichogamy, and large size. On the other hand, the forms which have enabled flowers most readily to avail themselves of the services of bees are the very characters which have been interpreted as adaptations for self-pollination and geitonogamy, viz., small size, homogamy, and the aggregation of dichogamous and other flowers in close clusters.

If an insect in search of nectar visits a diœcious or other diclinous plant, it is not hard to understand how it is likely to visit both staminate and pistillate flowers and readily effect cross-pollination. It is not so certain that a female bee in search of pollen will visit the pistillate flowers in anything like the same degree. Indeed my observations lead me to believe that they do not. I have seen hive-bees in great numbers collecting the pollen of *Salix humilis* and paying no attention to the pistillate flowers. They fairly monopolized the staminate flowers, while the pistillate flowers were visited by an entirely different set of insects. In the table there are six species of bees which get their pollen exclusively from diœcious species, Salix and *Spiræa Aruncus.* Of the plants furnishing pollen to oligotropic bees, these are the least able to utilize these bees on account of their diœcism.

Dichogamous flowers are at somewhat of a disadvantage in utilizing pollen-collecting bees from the fact that the bees are more apt to pay attention to the flowers which are discharging pollen and neglect those in the other stage. In *Impatiens fulva* and *I. pallida* I have observed that *Megachile brevis* collects the pollen from flowers in the first stage and avoids those with receptive stigmas, because she instantly perceives that the anthers are gone. *Apis mellifica* and *Bombus virginicus* do the same when collecting the pollen of *I. fulva*. In *Campanula Americana*, which is also proterandrous, the oligotropic *Megachile exilis* cleans the pollen from the style-brushes before the stigma opens, and avoids the old flowers. In *Lobelia syphilitica* I have seen little bees collecting the pollen which was pushed out of the anther tube before the stigma appeared. In the proterandrous *Monarda Bradburiana* I have seen small bees collecting pollen directly from the anthers, avoiding the old flowers. The strongly dichogamous flowers mentioned in the table are not so well adapted to utilize their special visitors as are the homogamous ones, such as Viola, Psoralea, Hibiscus, Cassia, because in the latter the bees cannot collect the pollen without touching the stigmas.

Some dichogamous flowers may make effective use of the pollen-collecting bees, as in the case of *Nymphæa reniformis*, which, in my opinion, is proterogynous and without nectar. By a sudden bending of the filaments, bees alighting on the anthers are let down into the stigmatic basin before they discover that the pollen is not being discharged. Of course, in other dichogamous flowers the bees may visit the flowers in the pistillate stage before they discover that the pollen is gone, or for nectar, but my observations have convinced me that this is not the rule, for if they do not know exactly what they are doing and how to do it, they act just like it. On their pollen-collecting expeditions they do not make many mistakes or waste much time.

Even some homogamous flowers are so large that the smaller bees may collect their pollen without touching the stigmas. This may not matter so much if the flowers are visited by large bees, which are more effective. But the smaller flower may, in many cases, utilize the large bees as well and the smaller ones better. So I think the influence of the pollen-collecting bees is in favor of the smaller homogamous flowers.

Under the influence of the nectar-sucking, less specialized, anthophilous insects the highest development is found in diclinous, dichogamous, and hercogamous flowers with highly specialized nectaries and precise localization of pollen contact. In the less specialized plants, this kind of adaptation early reached the highest degree of perfection in the case of the orchids. But, as far as I know, no orchid holds an important relation in the economy of any bee.

Under the influence of the female bees, the most highly specialized of anthophilous insects, the highest development is found in homogamous flowers without nectar, such as Desmodium and Cassia.

Since bees have entered the field, many flowers seem to have been at a disadvantage in gaining their services, because the stamens were so few that they could not offer pollen in paying quantities. And in many cases the stamens were covered by galeæ and carinæ, so that, to collect the pollen, the bee would have to spend much time going to the bottom of every flower. This difficulty was obviated by lengthening the stamens, reducing the size of the flowers, and crowding the flowers so that the bees could run over or around the inflorescences and sweep up immense quantities of pollen. Inflorescences of this kind are found in Cornus, Hydrangea and Viburnum.

Here we find an explanation of the fact that certain Leguminosæ and Labiatæ have abandoned their galeæ and carinæ, exposing their stamens, and contracting their infloresences into head-like or flat-topped clusters, as in Amorpha, Petalostemon, Lophanthus, Mentha, Blephilia, and Pycnanthemum. Contrary to Müller, I think Delpino is right in regarding Mentha as one of the most highly specialized of the Labiatæ, and I incline to the same opinion regarding the above genera of Leguminosæ. These cases are obscured by the fact that the arrangements permit the visits of a lot of less specialized insects. Nevertheless I think the bees have determined the result.

In the case of Lobelia I have mentioned that small bees collect the pollen pushed out of the tube before the stigma appears. In the Compositæ we find plants perhaps best adapted to attract and utilize the pollen-collecting bees, and the table shows that they have among their visitors more oligotropic bees than any other group of native plants, and that, too, in spite of their dichogamy. If the flowers were greatly scattered, they no doubt would not attract so many bees, and the bees could carry off the pollen and not render any service by visiting the flowers after the stigmas appeared. But, as a result of the reduction of the flowers in size and the crowding of them in heads, we find a circle of flowers, each one of which ejects the contents of five anthers in a convenient mass. Just without is a circle of flowers with protruding stigmas. Bees sweep over the disk, filling their pollen-scopæ with the greatest facility, at the same time effectually pollinating the neighboring stigmas.

As the homogamous flowers have largely been given over as adaptations to autogamy, so the crowded inflorescences have been given over as adaptations to geitonogamy. As a category I do not accept Kerner's *geitonogamy*. Kerner regards most of the crowded inflorescences as adaptations for geitonogamy, and founds a special category for their reception. This is accepted by Knuth and is incorporated in his recent Handbuch.[7] I do not believe in any adaptations for geitonogamy. I do not deny that it occurs, and under pseudo-ecological conditions may be advantageous, but it is only the name of an accident and does not account for any floral adaptations. Kerner does not make a distinction between a structure, or habit, which has a certain effect, and one which may be conceived to be developed for a certain purpose, or selected on a certain condition. He even speaks of a "contrivance for securing hybridization." Under "contrivances whereby the pollen is protected against wet" he says: "In *Podophyllum peltatum* the pollen is sheltered by the bell-shaped flower, but in addition to this the peltate foliage-leaves are also spread out over the flowers and act as umbrellas." Under the category of protection by isolation in water he mentions a number of ordinary water plants and says: "Flies and beetles which come through the air for honey and pollen are welcome visitors, promoting, as they do, a crossing of the pollen; snails, centipedes, etc., are, on the other hand, kept

[7] Handbuch der Blütenbiologie 1 : 51.

back by the water." He gives no evidence that this protection has anything to do with the fact that the plants have acquired an aquatic location. He uses trivial and accidental effects as a basis for interpretation of all kinds of ecological phenomena.

While it is true that adaptations for cross-pollination are more apparent in the less specialized plants depending on the less specialized anthophilous insects, it does not follow that the adaptations of the highest plants in relation to the highest insects, though more obscure, are to be interpreted as arrangements for autogamy and geitonogamy.

V. *On the supposed pollen-carrying apparatus of flies and birds.* —In regard to the plumose aristæ of such genera of Syrphidæ as Volucella and Sericomyia, Loew[8] observes that the structure appears of no use to the flies, but is of importance in the transfer of pollen. And he regards them, as well as the hairy coat on the lower part of the face, as an adaptation for carrying pollen. In the same connection he mentions the hairy eyes of certain species, though he does not go so far as to consider this as an adaptation for the same purpose.

In the *Entomological News* **4**: 323. 1895, under the title *Insects as pollenizers*, Mr. J. B. Smith mentions that some Diptera have compound hairs, similar to those found in the Apidæ. The author does not say exactly what he does mean, but I have always regarded the note as implying the view that these hairs were so modified for carrying pollen.

In the *American Naturalist* **28**: 680–681. 1874, Mr. J. L. Hancock speaks of certain "repositories" on the head of the ruby-throated humming bird, and throughout his paper seems to imply that the feathers, etc., are specially modified for carrying pollen. As Mr. Darwin says, proof of the existence of such adaptations would be fatal to the theory of natural selection. I have always regarded these statements as mere teleological curiosities, but in his *Handbuch* Knuth has adopted Loew's views.

[8] Jahr. Bot. Gartens Berlin **6**: 114. 1886.

which has the effect of giving them some standing among the fundamental principles of flower-and-insect ecology.

The existence of branched hairs in the bees may properly be interpreted as an adaptation for carrying pollen, because the bees use them for that purpose, and the importance of the hairs is evident, in view of the economy of the insects. They cannot in any way be interpreted as existing for the benefit of the flowers. It could be of no advantage to flies and birds to carry pollen, since they make no use of it. However, it might be claimed that these guests derived an indirect benefit from the pollination of their favorite plants. But their relations to flowers are not close enough to make their existence depend upon the pollination and preservation of any particular species.

An examination of the inquiline bees will lead to the conclusion that the several genera are not related to one another but have arisen independently from different groups of host bees. It will also lead to the conclusion that they have all lost their hairy coats, or tend to do so, as in Psithyrus. To my mind the fact that these bees began to lose their coats as they abandoned their pollen-collecting habits, involves a clear refutation of the claims that any structures on flies and birds were developed for the purpose of carrying pollen.

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